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MORPHOLOGY AND ANATOMY OF THE SAURURACEAE.

I. FLORAL ANATOMY AND EMBRYOLOGY¹

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ABSTRACT

The present paper deals with certain aspects of morphology and anatomy of the Saururaceae. Floral anatomy and embryology suggest a close relationship among the genera. In floral anatomy the genus *Saururus* is the least specialized and *Anemopsis* the most highly specialized. Structure and morphology of inflorescence and also flower suggest the manifestation of certain evolutionary trends, probably guided by reduction, cohesion and adnation. Origin of inferior ovary in the Saururaceae is discussed. Carpels and nature of placentation show certain primitive features. Origin and evolution from apocarpous condition to syncarpous condition of carpels are briefly discussed. Further details will be presented in a separate paper. M. V. S. RAJU, Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada.

INTRODUCTION

The Saururaceae has been one of the long-neglected angiosperm families in the field of morphology and anatomy. A perusal of the literature shows that earlier investigations have been superficial. In several discussions of comparative morphology and anatomy of the families of the order Piperales and other allied orders, some of the old descriptions of the Saururaceae have been considered. Very often, the family Saururaceae and its composition and affinities have been discussed without much detailed work. In view of this lack of sufficient information, an attempt has been made to investigate in detail some of the salient morphological and anatomical features.

The Saururaceae, according to present knowledge, consists of 6 species—*Saururus cernuus* L., *S. chinensis* (Lour) Baill., *Houttuynia cordata* Thunb., *Anemopsis californica* Hook. & Arn., *Gymnotheca chinensis* Decaisne., and *G. involucrata* P'ei. No material of the last genus was available for this investigation. However, at various stages of description and discussion, previous reports on *Gymnotheca* have been taken into consideration. The present paper deals with floral anatomy and embryology and other related features of the Saururaceae.

Members of the family Saururaceae are perennial aromatic herbs inhabiting moist places. The spirally arranged simple leaves are stipulate (Figs. 1, 5, 8). In *Houttuynia* the stipules are prominent, often enclosing a part of the internode

¹ An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as part of a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

above the node (Fig. 8). In the other genera, they are not prominently visible but are adnate to the petiole and form a sheath around the node as in monocots. The leaves of *Saururus*, *Gymnotheca* and *Houttuynia* are auriculate to lanceolate and palmately net-veined. In the case of *Anemopsis*, leaves are elliptic-oblong with a conspicuous mid-vein.

INFLORESCENCE

The inflorescence of the Saururaceae is either a terminal spike or a raceme (Figs. 1, 5, 8). In *Saururus* the naked bracteate flowers are often arranged in pairs, a feature which distorts their spiral arrangement. The flowers are adnate to the subtending bract in earlier stages of growth. The flowers of *S. chinensis* are much more sparsely arranged than those of *S. cernuus*, but in most other respects, the inflorescences of the two species are similar (Figs. 12, 13).

The inflorescence of *Houttuynia cordata* has been described in detail by Nozeran (1955). It is a spike with 4 conspicuous bracts at the base (some flowers, however, have small pedicels). Bracts higher up are much reduced to either scales or simple enations. The flowers show various degree of adnation of their pedicels with the bracts. However, in most cases this adnation is not superficially recognizable (Figs. 9, 15). In this species, Nozeran (1955) has reported a progressive transformation of complete flowers into staminate and pistillate ones within the same spike. Similar transformation has been observed by the present author.

Structures of both flower and inflorescence of *Anemopsis* have been described by Quibell (1941). The inflorescence is a highly condensed spike and is subtended by 6–8 petaloid bracts. The young inflorescence axis in early stages resembles a flower covered by bracts. The inflorescence axis is mainly made up of "sunken" pistils (Fig. 16). The bracts, which vary in number, are foliaceous and gradually decrease in size from base upwards (Fig. 5). Except for the lowermost bracts, the rest are adnate to naked flowers.

The inflorescence of *Gymnotheca chinensis* is also a spike, if one follows the terminology of Nozeran (1955). The bracts are not so conspicuous as those of *H. cordata* and *A. californica*. However, the gradual reduction in size of bracts from base upward is similar to the situation in *H. cordata*.

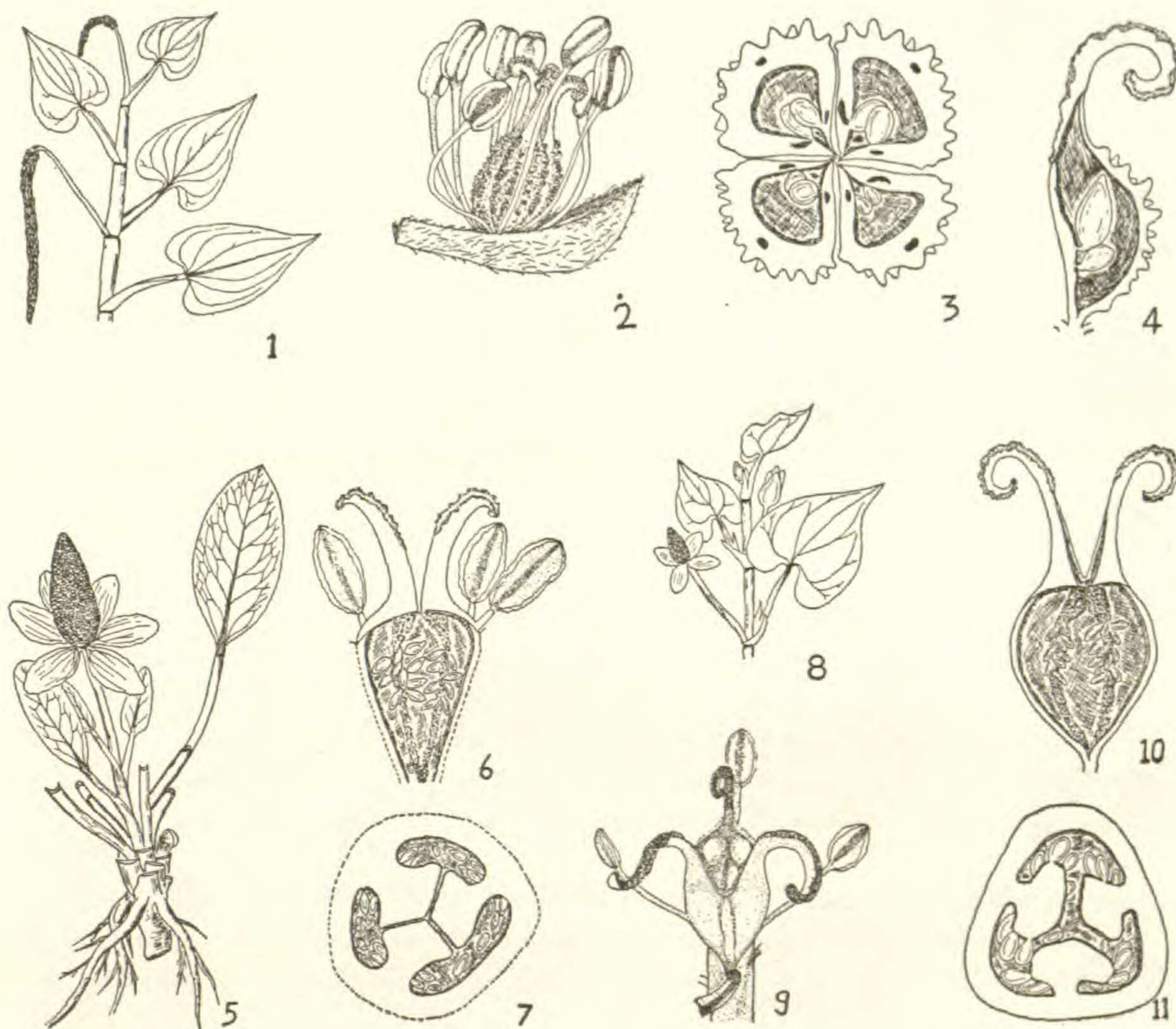
FLOWER

Flowers of *Saururus*, particularly *S. cernuus* show considerable variation in structure and number. An average flower of *S. cernuus* is pedicellate with 4 simple pistils and 6 stamens. Other combinations like 4–5, 4–7, 4–8, 5–7, 5–8, 3–4, and 3–6 have been observed. Serial sections of flowers of *S. cernuus* show the spiral arrangements of carpels and stamens. Carpels are very closely approximated to one another giving an impression of syncarpy. The stamens are hypogynous and are opposite the carpels (Fig. 2). Pistils show extensive stigmatic crests on adaxial sides of styles (Figs. 2, 4). The stamens are much longer than the styles. In *S. chinensis* flowers show the same variation as *S. cernuus*, but the pistils have shorter styles. Stamens in *S. chinensis* are perigynous and do not exceed the pistils in height.

In *Houttuynia cordata*, the flowers are naked and have small pedicels. These

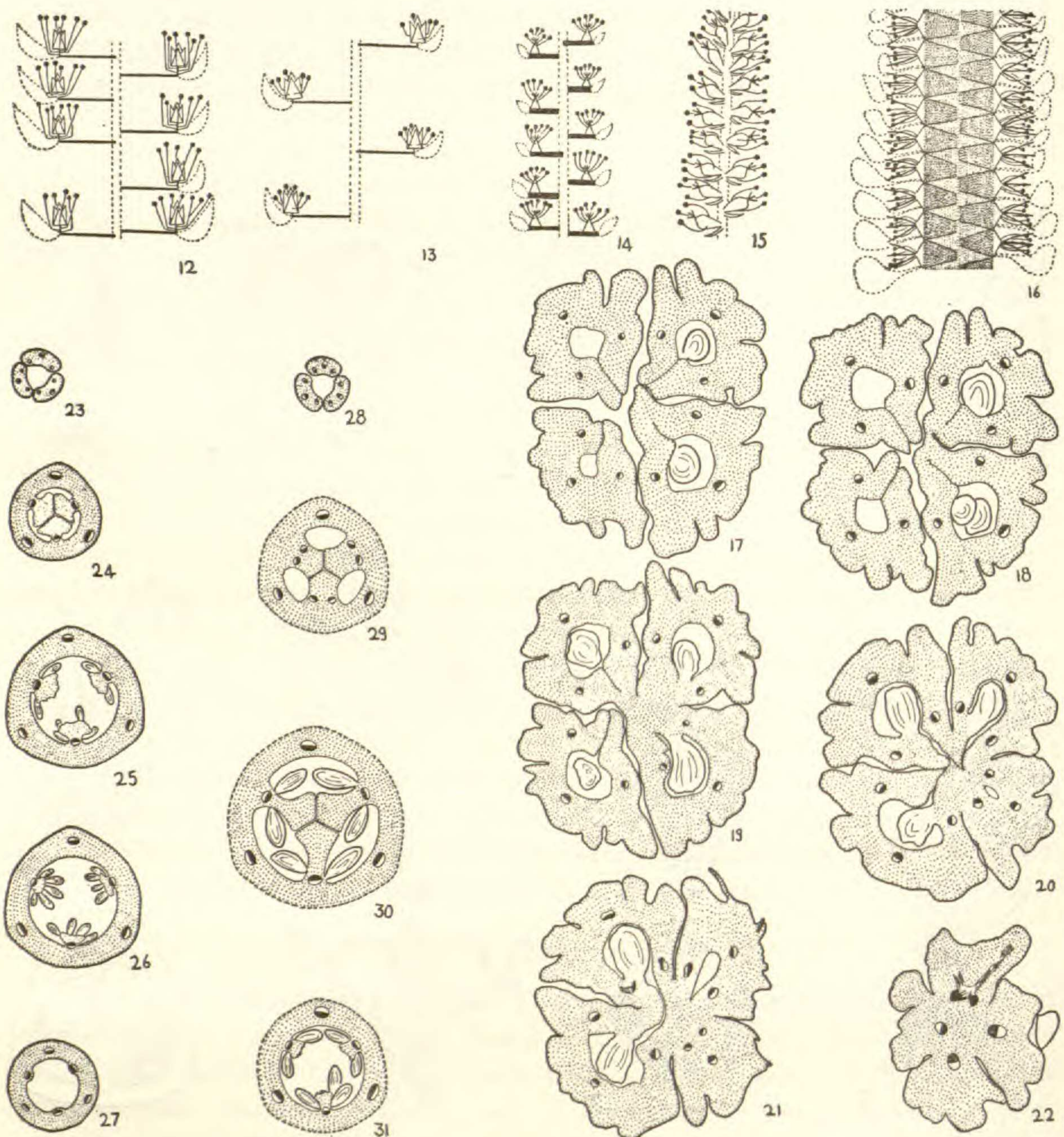
pedicels toward the inflorescence apex are further shortened or the flowers are sessile. The compound pistil is made up of three carpels, and the styles are free with wide stigmatic crests on their adaxial sides (Figs. 9, 10). In the arrangement of flowers, *Gymnotheca* resembles *Houttuynia*. According to the diagram of Decaisne (1845), the flower of *Gymnotheca chinensis* has a 4-partite pistil and 6 epigynous stamens (Fig. 14).

The inflorescence of *Anemopsis californica* has pistils buried in the "inflorescence axis". In these naked flowers, the compound pistil is made up of usually 3 carpels with free styles. The epigynous stamens are usually six in number. However, this number is subject to variation. The petaloid bract appears to be situated



Text Fig. 1. Figs. 1-4. *Saururus cernuus*. Fig. 1. A portion of branch showing the spiral arrangement of leaves and terminal inflorescences. Fig. 2. A flower with bract, stamens and pistils (note the warty structures on ovary). Fig. 3. Sectional view of pistil to show the position of ovules and vascular traces. Fig. 4. Longisection of a carpel. Figs. 5-7. *Anemopsis californica*. Fig. 5. A small plant with roots, rhizome, rosette of leaves and an inflorescence. Fig. 6. Longisection of ovary showing placentation, flared margins of stigmatic crest and epigynous stamens. Fig. 7. Transection of same showing parietal placentation and incomplete septa. Figs. 8-11. *Houttuynia cordata*. Fig. 8. A portion of branch with leaves, stipules and inflorescence. Fig. 9. A flower with a compound pistil and epicarpellary stamens. Short pedicel of flower is adnate to scale-like bract. Fig. 10. Longisection of pistil showing placentation and stigmatic crest. Fig. 11. Transection of ovary showing parietal placentation.

at the neck of the compound pistil. Developmentally it is adnate to the pistil along its length (Fig. 49). It is also interesting to note that in certain inflorescences bracts show a gradual change from base upwards from a petaloid bract to a petaloid stamen. This also followed by a highly reticulate venation pattern in the lowest bract to a highly reduced "dichotomous pattern" in bracts at the tip of inflorescence.



Text Fig. 2. Figs. 12-16. Diagrammatic sketches of portions of inflorescences of *Saururus cernuus*, *S. chinensis*, *Gymnotheca involucrata*, *Houttuynia cordata*, and *Anemopsis californica* respectively. Figs. 17-22. *Saururus cernuus*—Transverse sections of flower (stamens not included) at different levels to show spiral arrangement of carpels and also placentation, $\times 80$. Figs. 23-27. *Houttuynia cordata*—Transection of compound pistil at different levels (diagrammatic). Figs. 28-31. *Anemopsis californica*—Transection of flower (stamens not included) at different levels (diagrammatic).

ANATOMY OF THE FLOWER

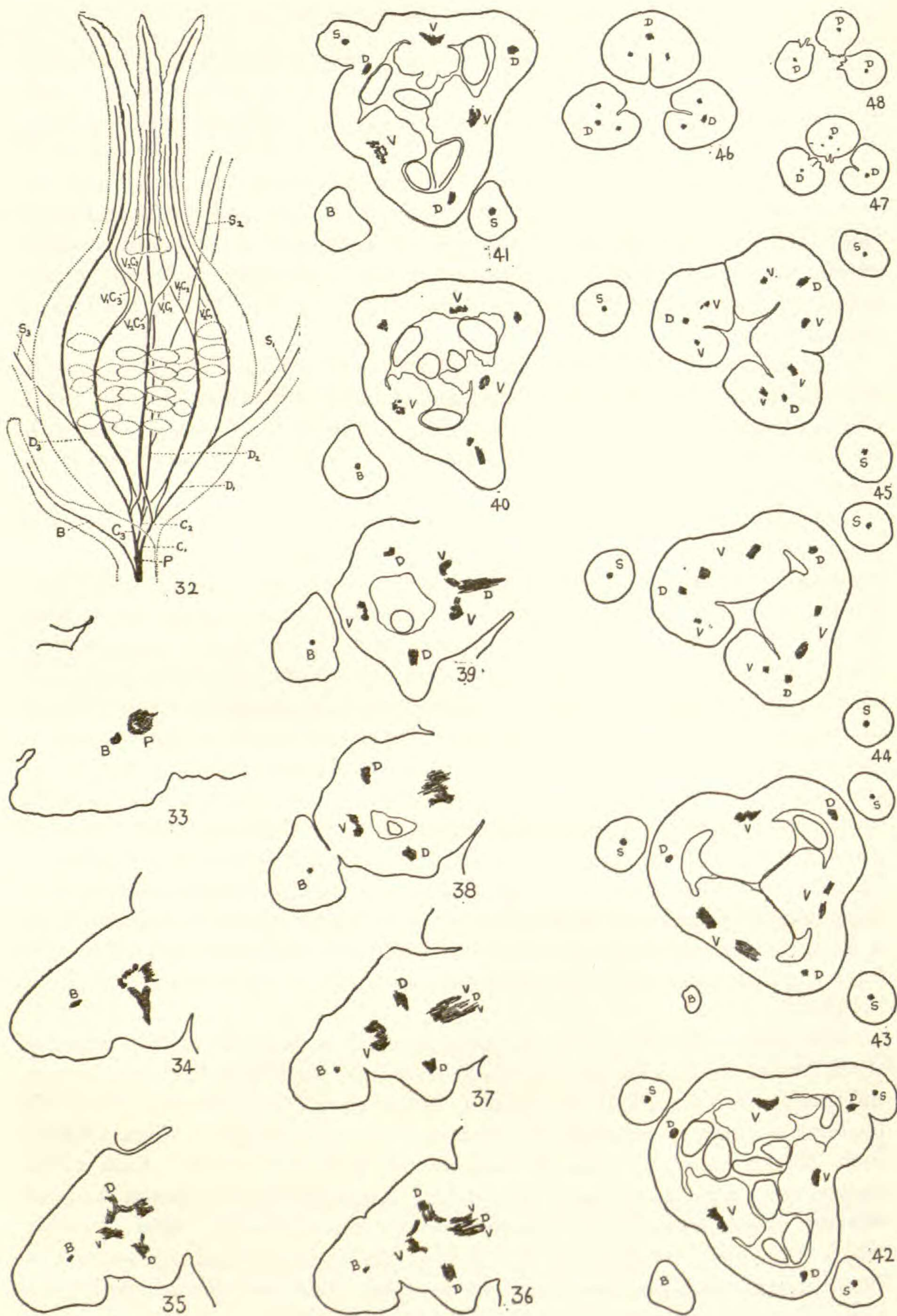
Saururus.—Anatomy of the flower has been recently described for *S. cernuus* by Murthy (1959). Carpellary traces* in the flower originate spirally. Serial sections also indicate the spiral arrangement of carpels. Although ventral margins of carpels are closely approximated or partially fused at the lowermost regions of 'pistil', the ventral traces remain free throughout their course. In certain cases the ventral and dorsal traces of each carpel merge at the apex and appear as though fused to form a common trace. It is also not uncommon to find ventral traces ending near the base of styles. Ventral traces give off branches to the two ovules present in each carpel; placentation in the carpel has been here interpreted as laminar (Figs. 3, 4, 17-22).

The anatomy of the flower of *Saururus chinensis* is similar to that of *S. cernuus* with, however, a few deviations. Stamen traces arise as branches from the dorsal traces of carpels. The ventral trace invariably merges in the stigmatic region with the dorsal trace to form a thick common trace. Unlike *S. cernuus*, there is no conspicuous style in *S. chinensis*.

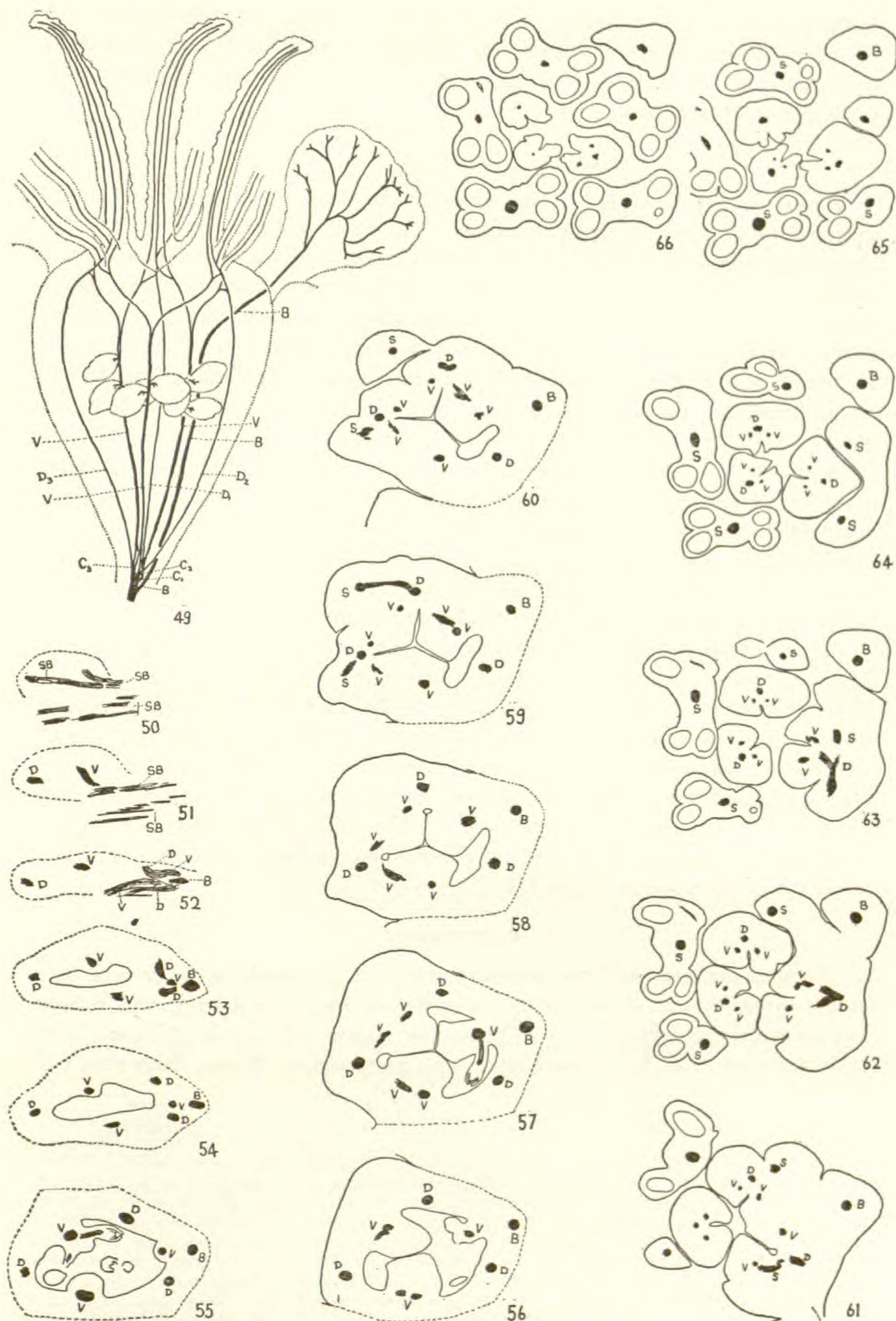
Houttuynia.—The naked flowers are trimerous and bracteate (Fig. 9). The vascular bundle from the inflorescence axis extends into the cortex and becomes the trace for the flower. It branches to form two traces, one leading into the bract and the other into the flower proper (Figs. 32, 33). The bract trace may or may not ramify depending on whether the bract is "leaf-like" or scaly. The remaining trace branches at different levels to form three independent carpellary traces which show a spiral arrangement (Fig. 32). Each carpellary trace gives rise to a dorsal and two ventral traces (Figs. 32, 34-39). The ventral traces of adjacent carpels fuse together to form "compound ventral trace" or placental trace. Each placental trace gives off branches which supply the ovules. The placental trace when it reaches the style bases separates and extends into the respective styles. Ventral traces together with the dorsal trace go into the style and all three remain separate. No instance of their fusion at the tip of style was found. Placentation is parietal and ovules are present only in placental region where the ventral traces have fused to form the placental trace. Stamen traces are formed much later than the ventral traces and arise about the middle of the pistil from the carpellary dorsal trace (Figs. 32, 40-48).

Anemopsis.—Quibell (1941) has given in sufficient detail the vascular anatomy of the flower. As in other genera, a single trace from the inflorescence axis diverges and branches to form a bract trace and a "flower trace" (Figs. 49-52). Although the bract is adnate to the pistil, the bract-trace is free throughout (Figs. 49-66). Each "flower trace" branches to form ventral and dorsal traces. Each carpel receives two ventral traces and a dorsal trace. As in *Houttuynia*, ventral traces of adjacent carpels immediately fuse to form the placental trace whose branches supply the ovules. At about the base of style, the placental traces separate to give ventral traces which pass into the respective styles. Each ventral trace, on its way

* For the sake of convenience the term 'trace' has been used in describing the vasculature of different organs of flowers.



Text Fig. 3. *Houttuynia cordata*. Fig. 32. Diagrammatic sketch of a flower showing vascular traces. Figs. 33-48. Transections of flower at different levels to show vascular anatomy of the flower (B, bract trace; C₁, 2, 3, traces of three carpels; D, dorsal trace of carpel; D₁, 2, 3, dorsal trace or common trace of dorsal trace of carpel and stamen trace; P, pedicel trace; S, stamen; S₁, 2, 3, stamen traces; V₁C₁, V₂C₁, V₁C₂, V₂C₂, V₁C₃, V₂C₃, ventral traces of respective carpels; V, ventral trace), $\times 100$.



Text Fig. 4. *Anemopsis californica*. Fig. 49. Diagrammatic sketch of a flower to show vascular traces. Figs. 50-66. Transections at different levels of a flower showing vascular traces (B, bract; C₁, 2, 3, carpel traces; D, D₁, D₂, D₃, dorsal traces; SB, axial bundle of inflorescence; S, stamen trace; V, ventral trace), $\times 100$.

to the base of the style, is connected with the dorsal trace. The dorsal trace with the other two ventral traces extend into the style (Figs. 58-66). At the base of style the dorsal bundle gives off branches to one or two stamens. Placentation is parietal as in *Houttuynia*.

CARPELS AND PLACENTATION

A considerable variation has been found in the structure of carpels and in the organization of pistils in the Saururaceae. Carpels in *Saururus cernuus* are free throughout except at the base, a little above the short pedicel where they show a lateral concrescence (Figs. 17-22). They arise in a spiral fashion, a fact clearly seen in serial sections. There is considerable elongation above the ovule-bearing region. In *Houttuynia*, *Gymnotheca* and *Anemopsis*, clearly recognizable stylar regions are found. Furthermore, in all these three genera, the pistil is "compound" (in the sense that the ovary is syncarpous and the styles are free) (Figs. 6, 7, 10, 11).

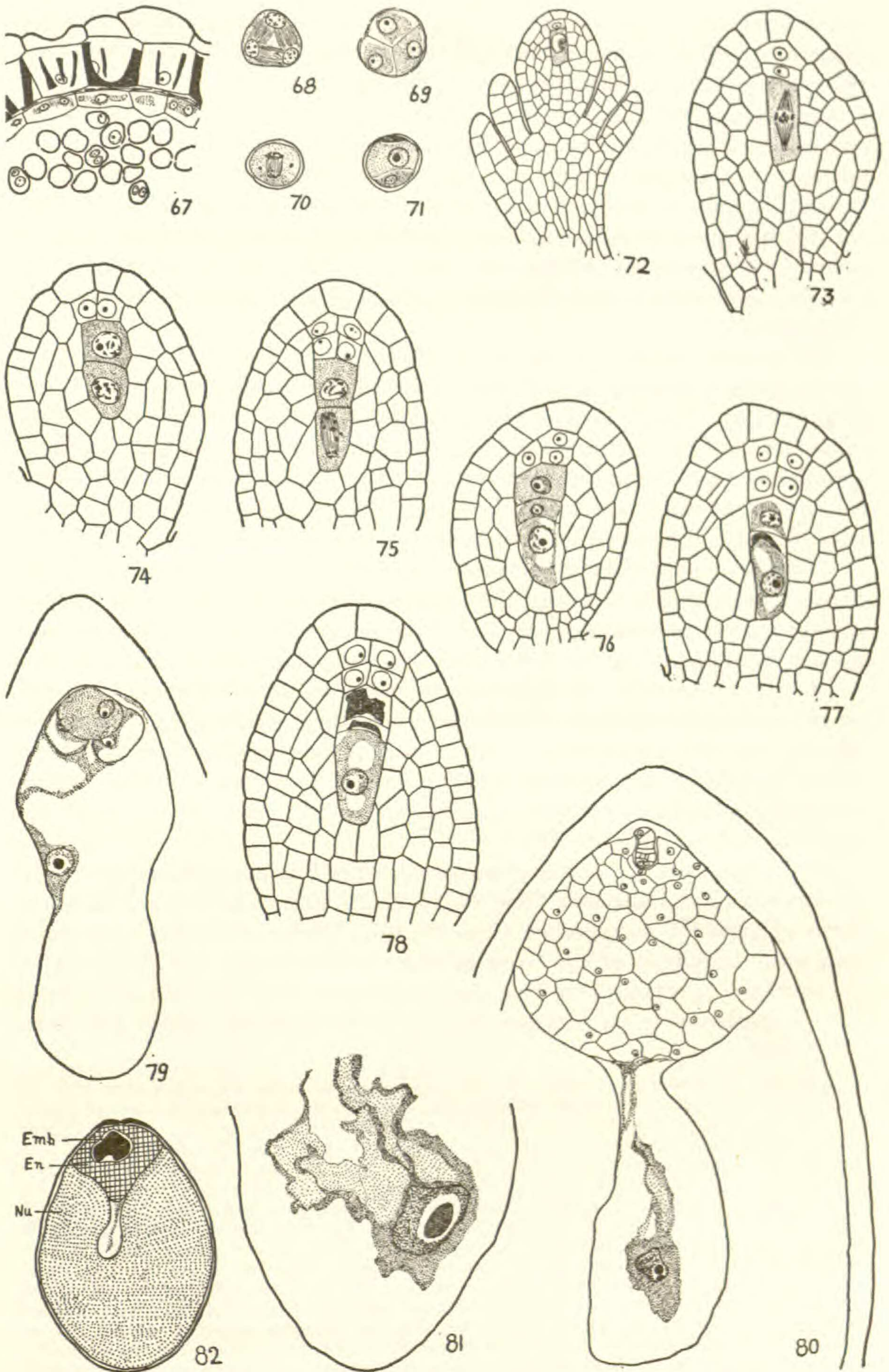
In *Saururus cernuus*, the folded laminae are conspicuous and the ventral traces are present away from the carpellary margins. During organization of the pistil, these laminar margins of adjacent carpels undergo concrescence which is to a considerable extent mistaken for axile placentation; placentation here is actually laminar. The lateral concrescence of adjacent carpels may be attributed to a case of "incipient syncarpous tendency" (Bailey and Swamy, 1951).

The compound pistil of *Houttuynia* and *Anemopsis* is formed as a result of lateral approximation and concrescence of carpellary margins of adjacent carpels. This concrescence is also accompanied by fusion of ventral traces of adjacent carpels. Only in this region of concrescence of carpellary margins and also of lateral or ventral traces is parietal placentation organized. The sterile margins of carpels also undergo concrescence to form septa; as a result the compound pistil appears to be three-loculed (Figs. 23-31). This kind of incomplete septation is found in the upper part of the pistil of *Houttuynia cordata*; it extends almost half the depth of the pistil in *Anemopsis*.

EMBRYOLOGY

Saururus cernuus.—Microsporogenesis and male gametophyte.—The wall of a young anther consists of four layers, an epidermis, hypodermal layer, middle layer and an innermost tapetal layer. The mature anther wall has an epidermis with cutinized outer wall, hypodermal layer with characteristic fibrous thickening and

Text Fig. 5. *Saururus cernuus*. Fig. 67. A portion of anther wall showing epidermis, hypodermal layer with endothelial thickening, crushed middle layer, and a tepetal layer, $\times 333$. Figs. 68-71. Stages in the formation of microspore, $\times 833$. Fig. 72. A young ovule showing megaspore mother cell and primary parietal cell, $\times 333$. Fig. 73. Nucellus showing division of nucleus of megaspore mother cell, $\times 666$. Fig. 74. Same at a later stage with a dyad, $\times 666$. Fig. 75. Shows division of lower dyad cell, $\times 666$. Fig. 76. A linear row of three cells or a "triad", the lowermost being the megaspore, $\times 666$. Fig. 77. Degeneration of middle cell of a linear "triad". Note vacuolation in the lowermost cell, $\times 666$. Fig. 78. The upper two cells of a "triad" have degenerated and the lowermost has become the functional megaspore, $\times 666$. Fig. 79. Mature embryo sac with the egg apparatus and secondary nucleus, $\times 666$. Fig. 80. Longisection of a young seed showing embryo, cellular endosperm and a lower caecum containing a hypertrophied nucleus, $\times 147$. Fig. 81. An enlarged view of a hypertrophied nucleus in a caecum, $\times 666$. Fig. 82. Longisection of seed showing cellular endosperm, embryo and perisperm (Emb, embryo; En, endosperm; Nu, nucellus or perisperm), $\times 35$.



tapetal layer with binucleate cells (Fig. 67). The sporogenous cells differentiate themselves into microspore mother cells which undergo meiosis and form first microspore tetrads and then microspores (Figs. 68-71).

Megasporogenesis and female gametophyte.—The crassinucellate ovules are orthotropous-bitegmic and borne on laminar placentae (Figs. 3, 4, 19-21). The micropyle is organized by both the integuments. The outer integument is two layered; the inner is three layered. A single hypodermal archesporial cell is differentiated in a young ovular primordium. It undergoes a transverse division to form primary sporogenous and parietal cells (Fig. 72). The primary parietal cell, by anticlinal and transverse divisions, forms a parietal tissue of about 8 superposed cells (Figs. 73-78).

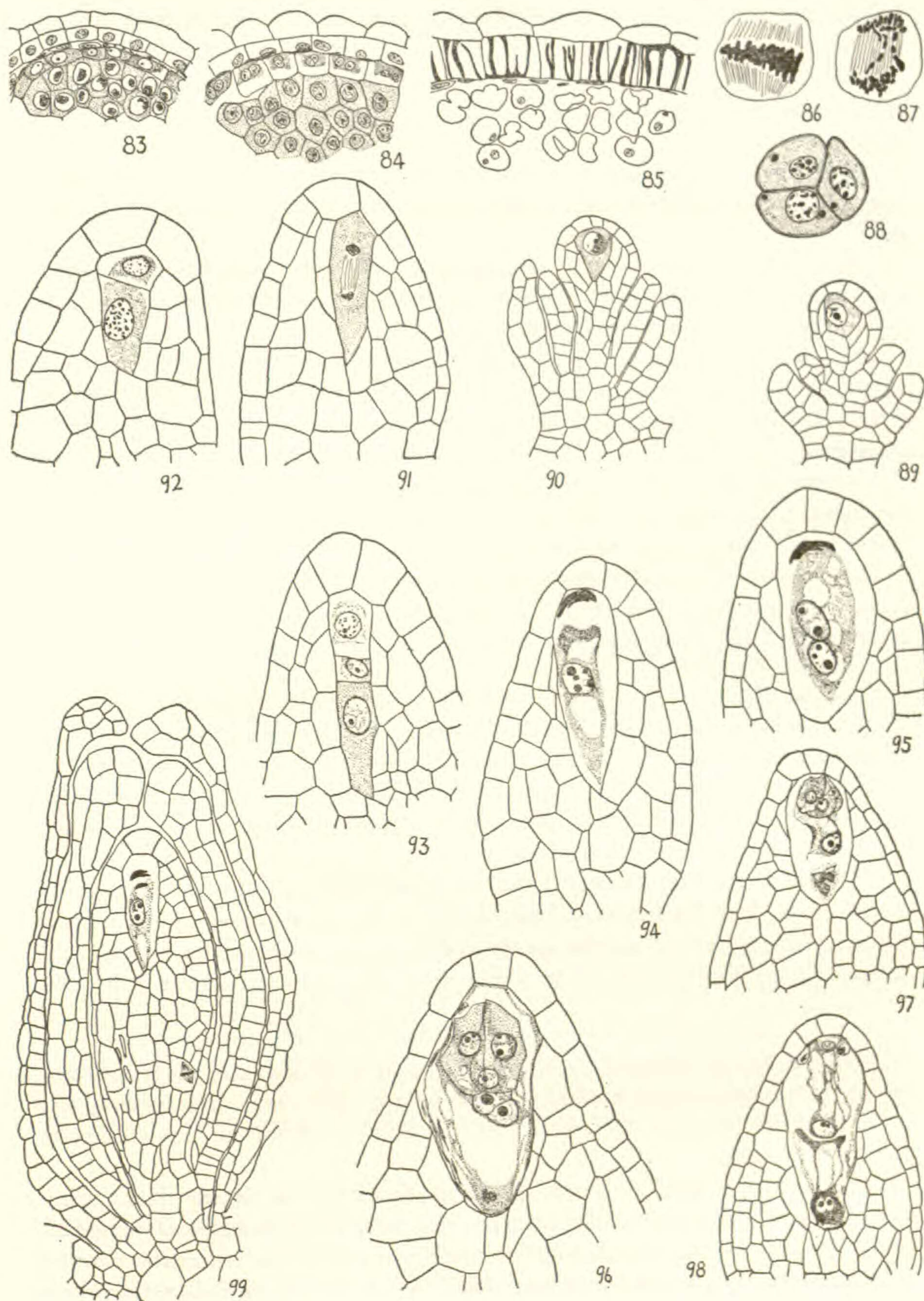
The primary sporogenous cell divides meiotically to form a dyad (Fig. 74). During further development, the lower dyad cell divides and the upper does not (Figs. 75-76). Thus, the dyad gives rise to a "triad" or a linear row of three cells (Figs. 76, 77). Of these three cells, the upper two degenerate and the lowermost develops into the embryo-sac (Figs. 77-79). The antipodal cells are ephemeral and seldom seen in a mature embryo sac. The egg apparatus is situated at the micropylar end and no case of fertilization was observed.

Endosperm.—The endosperm nucleus divides transversely to form a micropylar chamber and a chalazal chamber. The chalazal chamber behaves as a haustorium and the nucleus becomes hypertrophied. The mature seed encloses massive perisperm and a little endosperm surrounding the developing embryo (Figs. 80-82).

Houttuynia cordata.—Microsporogenesis and male gametophyte.—Microsporogenesis and male gametophyte development follow the sequence given for *Saururus cernuus*, but with some differences. Division of the microspore mother cell shows various cytological abnormalities resulting in the formation of sterile pollen. Frequently, micronuclei are seen in microspore tetrads. Very rarely free microspores are observed (Figs. 83-88).

Megasporogenesis and female gametophyte.—The bitegmic orthotropous ovules are borne on parietal placentae (Figs. 25, 26, 89-90, 99). The ovular primordium shows a hypodermal archesporium (Figs. 89, 90). Similar to *S. cernuus*, the outer integument is made up of two layers and inner of three layers (Fig. 99). Again, the micropyle is organized by both the integuments (Fig. 99). An archesporial cell of hypodermal origin functions directly as the megaspore mother cell (Figs.

Text Fig. 6. *Houttuynia cordata*. Fig. 83. A portion of anther showing anther wall and sporogenous tissue; anther wall shows epidermis, hypodermal layer, crushed middle layer and tapetal layer, $\times 333$. Fig. 84. Same at a later stage; note binucleate tapetal cells, $\times 333$. Fig. 85. Mature anther wall showing endothelial thickenings in hypodermal layer; note also microspores, $\times 333$. Fig. 86. Metaphase I in microspore mother cell, $\times 666$. Fig. 87. Same showing anaphase I; note the irregularity in the movement of chromosomes, $\times 666$. Fig. 88. Microspore tetrad with a few micronuclei, $\times 666$. Fig. 89. Ovular primordium with integumental and archesporial initials, $\times 333$. Fig. 90. A later stage of the same, $\times 333$. Fig. 91. First division of archesporial cell, $\times 666$. Fig. 92. A portion of nucellus showing a dyad, $\times 666$. Fig. 93. Same showing the lower cell has divided to form a linear row of three cells, $\times 666$. Fig. 94. Uninucleate embryo sac with degenerated upper dyad cell and megaspore, $\times 666$. Fig. 95. A binucleate embryo sac, $\times 666$. Fig. 96. An embryo sac showing hooked synergids, egg, two polar nuclei and degenerated antipodal cells, $\times 666$. Fig. 97. A mature embryo sac with egg apparatus, secondary nucleus and antipodal cells, $\times 333$. Fig. 98. A stage showing probably zygote; first division of endosperm nucleus has resulted in two cells, the lower one being a haustorium, $\times 333$. Fig. 99. A young ovule showing the developing megaspore, massive nucellus, and two integuments, inner three-layered and outer two-layered, $\times 133$.



91-98). The megaspore mother cell divides meiotically to give a linear row of three cells of which the lowermost is the megaspore that develops into the embryo sac (Figs. 91-98). Antipodal cells in the mature embryo sac are epheremal but in some cases these cells are seen in mature embryo sacs (Figs. 96-97). The egg apparatus in the micropylar end is made up of an egg cell and two hooked synergid cells (Fig. 96). Here, also, fertilization stages were not observed.

Endosperm.—The endosperm behaves as in *S. cernuus* (Fig. 98). In mature seeds often only endosperm and perisperm were observed. The embryo was not seen.

Anemopsis californica.—Microsporogenesis and male gametophyte.—Microsporogenesis and development of male gametophyte simulate those of *Saururus cernuus* and *Houttuynia cordata* (Figs. 100-105).

Megasporogenesis and female gametophyte.—The orthotropous bitegmic ovules are found on parietal placentae as in *H. cordata* (Figs. 6-7, 30-31). A hypodermal archesporial cell is differentiated and divides to form a parietal cell and primary sporogenous cell (Fig. 106). The primary sporogenous cell divides meiotically to give a row of three cells as in other genera (Fig. 107). The lowermost cell functions as the megaspore and develops into an embryo sac (Figs. 107-110). Stages in fertilization have not been observed.

Endosperm.—The earlier stages of endosperm development are like those of *Houttuynia* and *Saururus cernuus*. In the mature seed, massive perisperm, degenerated embryo and endosperm were observed.

FRUIT

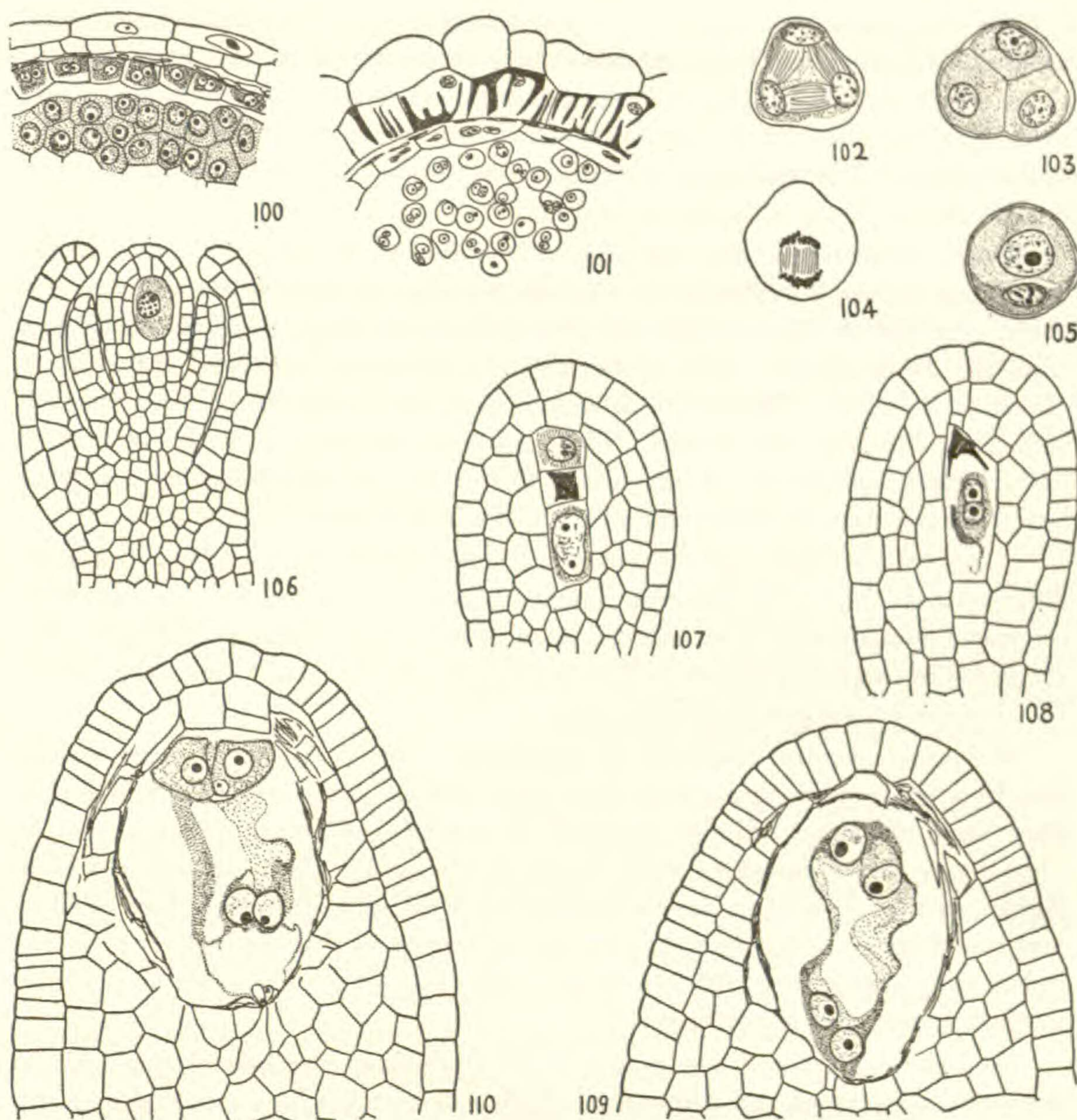
In *Saururus* simple pistils organize the fruit. The pericarp becomes dry-fleshy enclosing a single seed. No case of fruit dehiscence has been observed. Furthermore, there is no stony endocarp developed in the pericarp. On the other hand, seed coat becomes very hard and often closely abutting the inner wall of pericarp. The fruit is here interpreted as a berry.

In *Houttuynia* and *Anemopsis* the fruits are dehiscent capsules with many smaller seeds. The dehiscence of fruit occurs at the apical region by the disintegration of fused ventral margins in the middle region of three free styles. In a dehiscent fruit a circular port is seen at the top of the ovary leaving the styles free.

DISCUSSION

Observations on inflorescence of the six species of Saururaceae show an interesting evolutionary trend, probably guided by two processes: 1. reduction, and 2. cohesion and adnation. Of the four genera, *Saururus* shows the least change by the above processes.

The "common stalk" of flower and bract shows various degree of reduction. In *Saururus* the "common stalk" is much elongated and shows stages of its reduction. Further reduction of the same has resulted in a condition seen in *Houttuynia* in possessing a recognizable "common stalk" (Figs. 12, 13, 15). *Anemopsis*, on the other hand, shows the final culmination where the pistils appear embedded in the "inflorescence axis" and the bract appears to be situated at the top of the ovary (Figs. 16, 49). In all genera this process of reduction is associated with



Text Fig. 7. *Anemopsis californica*. Fig. 100. A portion of anther wall showing epidermis, hypodermal layer, crushed middle and tapetal layers surrounding the sporogenous tissue, $\times 333$. Fig. 101. same at a later stage showing endothelial thickenings in the hypodermis; two-celled microspores are seen, $\times 333$. Figs. 102-105. Stages in the formation of microspores, $\times 666$. Fig. 106. A young ovule showing megaspore mother cell and two integuments; note parietal cells, $\times 333$. Fig. 107. A portion of nucellus showing a linear row of 3 cells of which the lowermost develops into an embryo sac, $\times 666$. Fig. 108. Same at a later stage showing a 2-nucleate embryo sac with upper two degenerated cells, $\times 666$. Fig. 109. A portion of nucellus with a 4-nucleate embryo sac, $\times 666$. Fig. 110. Mature embryo sac with egg apparatus, two polars and 3 degenerating antipodals, $\times 666$.

concomitant cohesion and adnation of floral parts. By a process of reduction in the number and cohesion of carpels, the polycarpellate condition seen in *Saururus* has resulted in the three or four carpelled syncarpous condition found in the other genera. This change has been accompanied by the adnation of stamens to carpels and is exhibited by *Houttuynia*, *Gymnotheca* and *Anemopsis*. The genus *Anemopsis* has an inferior ovary, a feature that has resulted by their "sinking into" the inflorescence axis.

The phenomena mentioned above may also be explained in the light of floral anatomy. Although the bract appears to be a simple structure, it is very difficult to see where the bract begins and where it ends. It is morphologically intriguing to consider the trace of the "common stalk" as a "compound" one of bract and flower pedicel. This condition has been interpreted in *Saururus cernuus* as a case of adnation of flower to bract, by Murthy (1959).

Present observations show that only the pedicel of the flower is adnate to the bract; this feature is evidenced by vascular anatomy of *Houttuynia* and *Gymnotheca*. In *Saururus*, *Houttuynia* and *Gymnotheca*, the bract tends to remain free from the flower proper. But, in the case of *Anemopsis*, however, the bract is adnate to the pistil. This feature is of secondary derivation for the bract trace is completely free from the flower. This secondary condition is, probably, due to "development sinking-in" of the pistil. It can also be interpreted as a case of lateral concrescence of compound pistils in the inflorescence.

In *Saururus cernuus*, stamen traces are formed before the carpellary traces are differentiated. But in *S. chinensis*, vascular anatomy indicates that stamens have originated subsequently from the dorsal carpellary trace. This specialization has proceeded in increasing degree in *Houttuynia*, *Gymnotheca* and *Anemopsis* where the stamens are perigynous or epigynous.

In *Saururus* ventral traces are as prominent as the dorsal traces; they remain free from one another throughout their course except at the stylar tip where they show signs of fusion. Similar behavior of ventral and dorsal traces is seen in *Houttuynia* and *Anemopsis*; their fusion in the stylar tip is seldom observed. Besides, in these two latter genera, ventral traces of adjacent carpels fuse to form a placental trace. *Anemopsis* shows a unique feature in that the ventral trace has independent connections with the dorsal trace (Fig. 49). The exact significance of these connections is not known.

To begin with, the flower gets a single trace from the inflorescence axis in *Saururus*, *Houttuynia* and *Anemopsis*. Such a feature has been reported in many angiosperms. Puri (1951) in his review paper suggested that highly reduced flowers received just one trace. Whether this condition is simple by primitiveness or by reduction remains to be critically examined. As far as the present observations go, it seems that traces of different organs have undergone fusion to form a single composite trace.

The Saururaceae show both hypogenous and epigynous conditions. The problem then arises as to how the epigynous condition has been achieved. The problem of origin of the inferior ovary has been highly debated for a long time. Douglas (1944) in her comprehensive review has discussed different views regarding morphology of the inferior ovary. Of the many views postulated, only two have remained prominent; they are appendicular and axial views.

It is beyond doubt that in all genera of Saururaceae except *Saururus cernuus* stamens have fused with the carpels. In *Houttuynia* and *S. chinensis* stamens are situated half way up on the pistil. *Anemopsis* and *Gymnotheca* have their stamens on the ovary just below the styles. These clearly show that concrescence of certain

floral parts (here stamens) with the pistils has given rise to epigyny. This is in support of the views expressed by van Tieghem (see Puri, 1951, 1952; Eames, 1931).

In *Anemopsis*, besides the fusion of stamens with the ovary, there is developmentally a concrescence of pistils resulting in a massive spike. This condition has given an impression that pistils have "sunken". Adnation of the bract, with its free trace, to the pistil is an additional evidence to show that the ovary wall is made up of tissues other than that of the ovary wall itself.

Prior to syncarpy and epigyny, profound morphological and anatomical changes have taken place in flowers of the Saururaceae. These changes have been well preserved in the genus *Saururus*. The carpels with their respective stamens are arranged "spirally". The last-formed carpel does not possess a stamen or stamens. This detail suggests that the flowers of *S. cernuus*, adnate to bracts, are not actually simple; they are, probably, derived from a structure similar to an "inflorescence". Absence of an axial tissue, development of a terminal normal or abortive carpel with or without a stamen or stamens, and close telescoping of simple pistils suggest that the flower is of the "sympodial type". Each flower then represented by a carpel with its own stamen or stamens. A similar analogy can be traced in the flowers of Chloranthaceae (Cardemoy, 1863; Hooker, 1890). However, this idea has been contradicted on the basis of the absence of supernumerary structures in the flowers of Chloranthaceae (Swamy, 1953).

The successive arrangements of simple pistils with their associated stamen or stamens lead to two problems—nature of epigyny or perigyny in a simple pistil and same in compound pistil. In the case of *Saururus chinensis* the stamen or stamens are perigynous. This can be interpreted as a case of adnation. Syncarpous gynoecium also shows perigynous and epigynous conditions. It is difficult to say whether the cohesion of carpels appeared first or adnation of stamens to carpels. Available evidences, however, show in the Saururaceae that adnation of stamens to carpels appeared first as exemplified by *S. chinensis*. So, the flowers of *Houttuynia* and *Anemopsis* suggest that they are made up of three independent flowers which have undergone phylogenetic fusion. This is also amply evidenced by floral anatomy.

The above interpretations further lead to the problem whether the pistil is appendicular or axial. Vascular anatomy shows that there is nowhere in the ovary a residual trace or an axis around which carpels are arranged. The vascular elements are completely used up by the differentiated carpels. It is on this basis that flowers of Saururaceae have been interpreted as condensed inflorescence of the "sympodial type" simulating to a considerable extent vegetative branches where sympodial growth prevails. Anatomical evidences do not, however, give a correct picture of inferior ovary. Developmental studies are necessary for the interpretation of inferior ovary in some members of Saururaceae.

The trends of specialization postulated by Bailey and Swamy (1951) for the ranalian carpel have recently been useful in interpreting some primitive carpels. Although carpels of *Houttuynia* and *Anemopsis* are quite specialized, the conduplicate nature is still present in their styles which have flared-out stigmatic crests.

Although ontogenetic studies have not been made, available observations indicate that the ovule-bearing capacity of the carpel has brought several modifications in its train. The closure of carpels has occurred in the basal or ovule-bearing part leaving behind an extensive stigmatic crest. The stigmatic crest is supplied by both dorsal and ventral bundles. This feature is seen in *Saururus*, *Houttuynia* and *Anemopsis*. In some of the carpels, particularly of *S. cernuus*, retraction of ventral traces from stigmatic region toward the ovule-bearing part may be noticed. This retraction leaves a short style between ovary and stigma. In the case of *S. chinensis*, the stigmatic crest is supplied by both ventral and dorsal traces; it is situated just above the ovule-bearing part. This progressive phylogenetic specialization leading to the formation of a style between stigma and ovary is exhibited by the carpels of *Saururus*, *Houttuynia* and *Anemopsis*.

Superimposed on the evolutionary specialization mentioned above there is concomitant lateral concrescence of carpels resulting in a compound pistil. Furthermore, the "spiral" arrangement of carpels becomes less and less clear. Thus, in the development of pistils, simple or compound, several independent trends of specialization have occurred simultaneously in the Saururaceae.

Placentation in the Saururaceae is of two types, laminar and parietal. Laminar placentation is found in *Saururus* and parietal placentation in *Houttuynia* and *Anemopsis*. Bailey and Swamy (1951) after an extensive survey of carpels in the Ranales have come to the conclusion that carpels with laminar placentation are primitive and show various trends of specialization leading toward other types of placentation. A detailed study of carpels of *Saururus* has shown not only a laminar placentation but also different degrees of incipient syncarpous tendencies. The carpellary margins undergo concrescence or close approximation. This concrescence of carpellary margins does not occur at one level since they are arranged spirally. Axial tissue that is seen at the base of carpels is actually a composite of different carpellary margins. As a consequence, the pistil appears to be compound with more than one locule. In fact, this condition probably led several taxonomists to interpret this placentation as axile (Bailey, 1958; Lawrence, 1951; Benson, 1957).

From this basic laminar placentation, parietal placentation of *Houttuynia* and *Anemopsis* can be derived. The presence of free styles in the pistils of the above two genera shows that lateral concrescence of adjacent carpels has occurred in the ovule-bearing parts of carpels. Closely approximated partitions appear in the locule of the ovary of *Houttuynia* and *Anemopsis*. These partitions are the fused ventral carpellary margins. In the ovule bearing part, ventral parts of carpels have been retracted considerably apparently to accommodate the ovules developing inside.

In the organization of syncarpous ovary from simple carpels in Saururaceae, the so-called classical "torus" is not involved. The evolutionary trend of specialization from laminar to parietal placentation involves: firstly, the fusion of ventral margins of adjacent carpels; and secondly, lateral concrescence of the same carpels. These are further influenced greatly by the ovule bearing capacity of a syncarpous ovary. In *Houttuynia* and *Anemopsis* the ovary becomes "multilocular". The

retraction of partitions within the ovary in the lower part may be due to the acquisition of ovule-bearing capacity of ovary. Normally, the ovaries of genera mentioned above show multilocular nature in the upper part of ovary and unilocular in the lower part. Intermediate conditions showing various stages of phylogenetic retraction of partitions are not infrequent.

Eichler (1875-78) interpreted the flowers of *Saururus* and *Houttuynia* as obdiplotemonous; flowers which had two whorls of three stamens each and the outer whorl had aborted. In the present investigation the above-said feature has not been observed. In *Anemopsis* and *Gymnotheca*, each flower is usually associated with six stamens. Anatomy of flower has shown that traces for stamens arise from the dorsal bundle of carpels. In addition to the above feature, the first formed carpels of *Saururus* usually possess two stamens each, the last formed does not develop stamens. The absence of correlation between the number of carpels and stamens, negates the possibility of recognizing two whorls of stamens. A similar view has also been advanced by Nozeran (1955).

In his comparative survey of floral structures Nozeran (1955) writes that "the spike of *Houttuynia* is not entirely an inflorescence and is not still a flower". Furthermore, he hypothesized that the lowermost bracts transform into perianth lobes. He also observed in inflorescence several instances of reduction in number of stamens and carpels. On the basis of above details, he derived the spike of *Houttuynia* from a homogeneous inflorescence which was composed probably of trimerous flowers. In the present investigation, however, all the details given by Nozeran (1955) were not found. There is no doubt that at the tip of the inflorescence, an ovary was often borne, but there has not been enough evidence at present to support Nozeran's hypothesis.

Embryological investigations show great similarities among the three species, *Saururus cernuus*, *Houttuynia cordata* and *Anemopsis*. Development of both male and female gametophytes are very similar. During development of female gametophyte the archesporial cell gives rise to parietal cells in *Saururus* and *Anemopsis*. These parietal cells are absent in *Houttuynia*. The development of the female gametophyte in all three species studied conforms to the monosporic type (as here interpreted). Some stages in the development of endosperm were observed in *Houttuynia* and *Saururus cernuus*. In both cases the endosperm is of the cellular type. The above two genera also show endosperm haustoria. The embryo in *S. cernuus* suggests that the first division of the zygote should be transverse. Seeds enclose a massive perisperm and a little endosperm surrounding the small embryo. Similar embryological features have been recorded by Johnson (1900) for *S. cernuus*.

SUMMARY

An account of floral anatomy and embryology suggests that the genera of Saururaceae are closely interrelated. Structure and morphology of inflorescence and flower are discussed in the light of anatomy.

Anatomical details indicate that the inflorescence-type seen in *Anemopsis* is more specialized than the type seen in *Saururus* or other genera. This has been

achieved, according to the evidences advanced, by processes of reduction, adnation and cohesion of various floral entities.

Some of the morphological aspects of ovary, carpels and placentation have been discussed. Embryological details are similar in all the genera investigated here.

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